# OBSERVATIONS ON COLONIAL BREEDING IN THE BLACK-HEADED WEAVER AND VIEILLOT'S BLACK WEAVER

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## INTRODUCTION

The observations reported here were carried out near Kampala between 1962 and 1966. The species involved, the Black-headed Weaver *Ploceus cucullatus bohndorffi* (Reichenow) and Vieillot's Black Weaver *Melanopteryx nigerrimus nigerrimus* (Vieillot), are the commonest weaver birds in that area. General descriptions may be found in Jackson (1938), Bannerman (1949), Chapin (1954) and Mackworth-Praed & Grant (1955). One of the most striking features of their biology is the frequent occurrence of colonies of both species in the same site. Questions as to why this happens lead to a consideration of the advantages of colonial breeding, which are uncertain. At the same time, since these weavers appear to be closely similar in habits and ecology, problems of inter-specific competition are raised. The data described throw some light on these problems.

## OCCURRENCE OF SHARED SITES

*P. cucullatus* and *M. nigerrimus* are typical colonial weavers. Colonies in the Kampala area were most often built in bamboo or trees near houses; cassia, eucalyptus, and palm being favoured most. When sharing a site, nests of the two species were not normally intermingled but formed distinct, although contiguous, colonies.

The formation of colonies of weavers containing two or more species is not uncommon. Various examples are mentioned in the literature (see especially Bannerman, 1949) and the following combinations were noted in this study: *Ploceus jacksoni* (Shelley) and *M. nigerrimus*; *Ploceus capitalis* (Latham) and *M. nigerrimus*; *P. aurantius* (Vieillot) and *P. jacksoni*.

The data of Table 1 were obtained during the course of a survey in which the study area was traversed by car and all colonies within sight of the road recorded. At the same time the number of potential breeding sites was estimated, a potential site being a tree or group of trees of species known to be favoured, separated from the nearest dwelling by not more than five yards approximately. This provided a conservative estimate, since weavers might occasionally nest in unusual sites and more than one colony of the same species be built in the same tree or group of trees. Nevertheless the number of shared sites (24) was considerably greater than that expected as a result of chance distribution of colonies among available sites (4.3). The difference is highly significant ($x^2 = 108$; $P < .0005$) showing that the occurrence of sharing is not due to a shortage of apparently suitable sites.

TABLE 1

FREQUENCY OF SITES SHARED BY *P.CUCULLATUS* AND *M.NIGERRIMUS* IN RELATION TO FREQUENCY OF UNSHARED SITES AND TOTAL NUMBER OF POTENTIAL BREEDING SITES

| | Sites occupied by *P. cucullatus* | Sites not occupied by *P. cucullatus* |
|---|---|---|
| Sites occupied by *M.nigerrimus* | 24 (4.3) | 6 (25.7) |
| Sites not occupied by *M.nigerrimus* | 33 (52.7) | 334 (314.3) |

(Note: figures in brackets are expected numbers assuming random distribution of colonies amongst available sites.)

*P. cucullatus* colonies in sites where *M. nigerrimus* was also present tended to be larger than those where this was not so. Thus in a sample of 24 shared sites colony size varied from about 20 to 120 nests with a mode of about 50, whereas in 28 unshared sites the size range was approximately five to 100 with a mode of 30. A simple explanation of this may be that large *P. cucullatus* colonies are more attractive to *M. nigerrimus* than smaller ones. A similar comparison cannot be made for the size of *M. nigerrimus* colonies because only five not sharing with *P. cucullatus* were recorded.

## COLONIAL BREEDING AND PROTECTION FROM PREDATION

Presumably by breeding together these two species share and enhance the advantages of colony formation, whatever they may be. The above evidence does not support the view that it is the advantage of the protective nature of the site alone which is relevant. It is true that weaver breeding sites generally appear to have protective features, such as siting over water, in thorn trees or near houses (which may serve to keep ground-based predators away), but if there is no shortage of such sites this cannot explain the formation of colonies or the sharing of sites by different species.

Perhaps the most widely accepted hypothesis about the origin and advantages of colonial breeding supposes that it confers the same increased protection as flock formation in general. Lack (1954) discusses this and quotes evidence in support, none, however, relating to weavers. More recently Patterson (1965) has produced impressive supporting evidence in the case of the Black-headed Gull *Larus ridibundus* (Linn.). The protective value of the colony is thought to derive partly from increased awareness of the approach of predators and partly from the occurrence of mobbing. Darling (1938) also suggests that synchrony in the breeding of colonial birds reduces losses by predation because it limits the length of the breeding period and so the time during which predators may attack eggs and young. This is discussed by Kruuk (1964), Patterson (op. cit.) and—in relation to the Quelea, *Quelea quelea* (Linn.)—by Lack (1966). The presence of synchronised breeding has been demonstrated in the present species (Hall, (1970), However these hypotheses assume the existence of high predation pressure. In fact attacks on weaver colonies seem remarkably infrequent. During many hours spent in watching these birds during the course of four years I witnessed only three and received first hand accounts of only a few more. Details are given below.

(i) King's College, Budo, 1964 (precise date not recorded).

All the members of one colony were seen to have left it and to be perching on a tree about 30 yards away. A small hawk (unidentified) was perching at the top of the tree containing the colony, making no attempt to attack the nests containing chicks. I was unable to stay long enough to see what eventually happened.

(ii) Near Kampala, November, 1965.

All birds (*P. cucullatus* only) suddenly left the colony on the approach of a large hawk, African Goshawk *Accipiter tachiro* (Daudin). The latter perched in the tree until a few minutes later a female weaver returned to the site and was attacked. Both birds flew out of sight, but ten minutes later a hawk (possibly the same bird) flew past with prey in its claws.

(iii) Near Budo, February, 1966.

A pair of crows *Corvus albus* Müller was seen attacking the nests in a colony of Black Weavers. They persisted in this in spite of vigorous mobbing by the weavers.

(iv) Budo, 1962 (reported to author).

A *M. nigerrimus* colony was attacked by a party of Casqued Hornbills *Bycanistes subcylindricus* (Sclater). The colony was completely destroyed and never re-occupied. (This may be compared with a report by Bannerman (1949) of a colony of *Melanoploceus tricolor* (Hartlaub) containing more than 500 nests which was completely destroyed in a few days by a variety of birds, including "kites, crows, vultures, goshawks, buzzards, a crested hawk eagle and especially a pair of harrier hawks.")

(v) Budo, 1963 (reported to author).

A single Casqued Hornbill attacked the nests in a mixed colony of Black and Black-headed Weavers. The bird was shot and did little damage. Hornbills were very frequent visitors to the school compound at Budo and it seems remarkable that these attacks were not more frequent.

Only three attacks ((i), (iv) and (v) above) were recorded during my four years' residence at Budo, where I should almost certainly have been informed of any which did occur. There were generally five active breeding sites and, allowing for two breeding seasons each year, the destruction of one colony in four years represents an average loss of only 2½ per cent. This is very small compared with losses which have been recorded for other species. Lack (1954) gives data showing that losses from all causes in open-nested nidicolous birds from laying of eggs to departure of young vary from 41 to 78 per cent, averaging about 55 per cent. Lack considers that in passerines three-quarters of losses are probably due to predation.

The concentration of nests in a colony and the impossibility of concealing them must much increase their liability to attack and the actual rarity of attacks implies the existence of an effective deterrent. The above evidence shows that this deterrent is not mobbing, since this occurred in one case only, but the fact that the hawks did not attack nests suggests that it may be the difficulty of dealing with them which deters predators. The fact that weaver nests hang from the ends of twigs must make it very difficult for heavier predators to attack. It is of interest that the only breeding success data given by Lack (op. cit.) for a bird with a suspended nest (the Orchard Oriole *Icterus spurius*) show a loss of only 20 per cent. It may be, therefore, that, rather than the colonial habit being a response to predation, it is the protective value of the weaver nest which makes colonial breeding possible and that the latter has evolved for some other reason.

## ECOLOGICAL CONSIDERATIONS

According to Gause's principle species which have identical or closely similar ecological requirements are unlikely to exist in the same habitat. *P. cucullatus* and *M. nigerrimus* are closely related—Moreau (1960) places them in the same genus—and have very similar habits, the details of breeding behaviour, for example, varying very little (Crook, 1963). Both are said to be predominantly granivorous (e.g. Crook, 1964; Mackworth-Praed & Grant, 1955). On the face of it, therefore, Gause's principle might seem to be contradicted in this case. Accordingly, in an attempt to gauge the degree to which ecological requirements differ, data relating to distribution and food preferences are presented below.

On the continental scale *P. cucullatus* is much more widely distributed than *M. nigerrimus*, which is limited to moister environments, and the same difference has been demonstrated on the local scale in Uganda (Hall, 1968). There *M. nigerrimus* is limited to areas containing forest, whereas *P. cucullatus* also exists in drier habitats. This implies a difference in ecological requirements.

Lack (1954) has shown that the numbers of many bird species are limited by shortage of food and it follows that differences in food preference must constitute an important factor governing the extent of interspecific competition. Little detailed evidence con-

cerning food preferences in the present species is available. Examination of the gut contents of eight adult male *M. nigerrimus* (March, 1966) revealed the presence of vegetable matter but not grass seeds in all but one and of abundant insect remains in all but one. In an adult male *P. cucullatus* collected on the same occasion and another collected in November, 1965 the bulk of food consisted of grass seeds with small trace of insect material. However A. D. Forbes-Watson (pers. comm.) reports contrary evidence from specimens collected in Liberia [sub-species *P. c. cucullatus* (Müller) and *M. n. castaneofuscus* (Lesson)]:

> "Only a single *P. nigerrimus* out of twenty-nine had insect fragments, and even this had seeds as well. Four out of eleven *P. cucullatus* had insect fragments (with no trace of vegetable matter).
>
> "Each morning flocks of *P. cucullatus* would be catching insects (mostly moths) attracted to our mercury vapour lamp, but I never saw *P. nigerrimus* doing this, though this latter species was the commoner."

Clearly the diet of these birds may be very varied.

Kear (1962) and Newton (1967) have shown that in British finches (Fringillidae) preferred size of seed taken is related to bill size. Marked differences in food selection were demonstrated between species differing by approximately 15 per cent in bill dimensions. Conversely Ward (1965) shows that seed size is the chief factor determining selection between different species of grass seed by the weaver *Quelea quelea*. Table 2 shows mean values for bill dimensions of *P. cucullatus* and *M. nigerrimus*. The differences between the species are probably large enough to be associated with significant differences in food selection.

TABLE 2

DIMENSIONS OF BILL IN *P.CUCULLATUS* AND *M.NIGERRIMUS*

| Species and sex | Length: (mm) mean | s.d. | Depth: (mm) mean | s.d. | Number in sample |
|---|---|---|---|---|---|
| *P.cucullatus* male | 16.1 | 0.8 | 12.1 | 0.8 | 18 |
| ,, female | 15.0 | 0.5 | 10.25 | 1.0 | 8 |
| *M.nigerrimus* male | 14.4 | 0.4 | | | 26 |
| ,, ,, | | | 10.1 | 0.5 | 18* |
| ,, female | 13.7 | 0.8 | 9.8 | 0.3 | 9 |

(* Note: obvious errors in measuring depth made it necessary to discard measurements taken from 8 of the sample of *M.nigerrimus* males.)

In the course of a trial colour banding project weavers were caught by means of a house trap baited with bread crumbs placed near breeding colonies. Male Black-headed Weavers only were attracted by this bait, a fact which indicates a difference in foraging behaviour and possibly in food preferences between these birds and females of the same species and both sexes of the Black Weaver.

This rather scanty evidence indicates that whilst ecological requirements must broadly overlap there are also definite indications of differences between the species, particularly in food preferences. A detailed study of food selection would be interesting.

## DISCUSSION

The evidence described shows that the association between colonies of *P. cucullatus* and *M. nigerrimus* is not fortuitous, pointing to the existence of some advantage of colonial breeding which may be shared by different species. The hypothesis that this advantage lies in the protective value of the colony is not supported by the evidence.

An alternative proposed by Crook (1964, 1965) links colonial breeding with flock formation for foraging purposes. It is shown that gregariousness, colonial breeding and the use of seeds as food are correlated in the weavers (Ploceinae), which include insectivorous solitary nesting forms. The suggested explanation is that food in the form of seeds is most efficiently exploited by birds foraging in flocks, whereas insectivores feed most effectively as individuals or in small groups. However this explanation disregards the fact that most colonial weavers, although mainly granivorous as adults, feed their young on insects. (It has been shown that the food of *M. nigerrimus* chicks consists almost entirely of insects (Hall, in press (*b*)). Close observation of females in a colony does not suggest that they are collecting food as a flock.

An interesting parallel is afforded by the British finches. Newton (1967) states that some of the cardueline finches nest in groups or "loose colonies" and relates this to the fact that they feed their young mainly on seeds for which they forage communally. Fringilline finches, on the other hand, feed their chicks on insects or other invertebrates, foraging individually, and always nest solitarily in territories; they are, however, social outside the breeding season, when their food consists mainly of seeds. Thus, as noted by Lack (1954), there is no necessary connection between flock formation outside the breeding season and sociality within it; in fact on the basis of Crook's theory one would expect these weavers to be solitary nesters, rather than the converse.

According to the hypothesis of Wynne-Edwards (1962) the primary function of social organisation in animals is to regulate numbers through the control of reproductive rate. Applied to colonial birds this would imply that the size and number of colonies would be limited in relation to the resources of the habitat, so that a sudden increase in population would not lead to over-production of offspring, because surplus individuals would be excluded from colonies. Weaver colonies are known to occupy the same sites for long periods and the establishment of new permanent colonies seems to be infrequent. The size of a colony appears to remain quite constant from year to year, although there is little exact data. However the occurrence of polygyny in the present species must nullify any regulative effect of relatively fixed colony size, since although males may be excluded from a full colony, there is no evidence that females are or might be.

Wynne-Edwards' hypothesis might explain the existence of mixed colonies as a means of mutually adjusting the numbers of two competing species to avoid over-exploitation of the habitat. This would imply that the numbers of the two species occupying shared sites would be inversely proportional: a large number of one would tend to be accompanied by a small number of the other. Analysis of data from 24 shared sites showed that this was not so.

This discussion leads to the somewhat negative conclusion that, whereas the evidence casts doubt on a widely accepted hypothesis explaining the formation of breeding colonies as applied to the present species, at the same time it lends little support to the two alternatives discussed. The one positive conclusion is that there is a definite relationship between the species leading to the sharing of breeding sites, which calls for explanation.

## SUMMARY

The paper discusses the relationship between the colonial weavers *Ploceus cucullatus* and *Melanopteryx nigerrimus* and the possible function of colonial breeding. Evidence is presented indicating that the sharing of breeding sites by the species is not fortuitous, suggesting the existence of an advantage in colonial nesting which may be shared by different species. Observations of predation on weaver nests are described, showing that attacks are remarkably uncommon and casting some doubt on the theory that the chief function of social breeding is to provide protection from predation. Two other theories

about colonial breeding do not seem adequately to account for the facts. Limited evidence is presented relating to competition between the species.

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